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NOTES ON GEOGRAPHIC DISTRIBUTION

# New record of *Platyrrhinus angustirostris* Velazco, Gardner & Patterson, 2010 (Chiroptera, Phyllostomidae) in Colombia and potential distribution

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**Abstract.** The systematic revision of the *Platyrrhinus helleri* clade, which was found to be a species complex, led to the elevation of some subspecies to species level and the description of *Platyrrhinus angustirostris* Velazco, Gardner & Patterson, 2010. The conservation status and threats to this species are currently poorly understood. We report a new record of this species, extending its distribution into west-central Colombia. We used WorldClim bioclimatic layers to model its potential distribution; the results indicate that areas with stable temperatures and substantial precipitation during the warmest quarter offer the best environmental suitability for this species. This information is important for the conservation of *P. angustirostris* and its tropical habitats.

**Key words.** Bats, conservation, geographic range, isothermality, precipitation, WorldClim

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## INTRODUCTION

*Platyrrhinus* Saussure, 1860 (Phyllostomidae, Stenodermatinae) is a genus of broad-nosed bats endemic to the Neotropics and represents one of the most species-rich genera within the family (Palacios-Mosquera et al. 2020; Simmons and Cirranello 2024). Species of this genus are widely distributed throughout the Americas, ranging from southern Mexico to northern Argentina (Velazco and Patterson 2008), and inhabit a broad altitudinal gradient, from sea level to elevations exceeding 3,000 m (Velazco et al. 2010, 2018). Twenty species are currently recognized, with six occurring in the Andes (*P. albericoi* Velazco, 2005; *P. angustirostris* Velazco, Gardner & Patterson, 2010; *P. dorsalis* (Thomas, 1900); *P. ismaeli* Velazco, 2005; *P. masu* Velazco, 2005; and *P. umbratus* (Lyon, 1902)), three in the Pacific lowlands (*P. chocoensis* Alberico & Velasco, 1991; *P. matapalensis* Velazco, 2005; and *P. nitelinea* Velazco & Gardner, 2009), four on the Brazilian shield (*P. lineatus* Geoffroy, 1810; *P. incarum* (Thomas, 1912); *P. recifinus* Thomas, 1901; and *P. fusciventris* Velazco, Gardner & Patterson, 2010), two in the Amazon Basin to the eastern slopes of the Andes (*P. brachycephalus* Rouk & Carter, 1972 and *P. infuscus* Peters, 1880) (Velazco and Patterson 2008; Velazco and Lim 2014; Velazco et al. 2018); two on the Guiana Shield to the southernmost point in the Brazilian Amazon (*P. aurarius* Handley & Ferris, 1972 and *P. guianensis* Velazco & Lim, 2014); and three in Central America and northwestern South America (*P. aquilus* (Handley & Ferris, 1972); *P. helleri* Peters, 1866; and *P. vittatus* (Peters, 1860)) (Velazco and Patterson 2008; Velazco and Lim 2014; Velazco et al. 2018).

Over the past decade, morphometric, morphological, and molecular studies have significantly enhanced our understanding of the systematics and taxonomy of *Platyrrhinus* (Velazco and Lim 2014; Palacios-Mosquera et al. 2020). *Platyrrhinus helleri* was historically regarded as a widely distributed species, occurring from Oaxaca and Veracruz in Mexico to Peru, Bolivia, the Brazilian Amazon, and Trinidad (Simmons 2005). However, analyses of the cytochrome *b* gene revealed the presence of multiple lineages within populations previously assigned to *P. helleri*, which led to the description of two new species—*Platyrrhinus angustirostris*

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and *P. fusciventris*—as well as the elevation of *P. incarum* to a full species (Velazco et al. 2010). Further analyses revealed that *P. guianensis* is also part of the *helleri* species group (Velazco and Lim 2014) and that *P. matapalensis* was described based on specimens initially misidentified as *P. helleri* (Velazco 2005).

*Platyrrhinus angustirostris* occurs in sympatry with *P. helleri*, *P. fusciventris*, and *P. incarum* (Velazco et al. 2010) and can be difficult to distinguish from these species due to overlapping morphometric traits. The species was described based on morphological characters that differentiate it from closely related taxa; however, its phylogenetic placement was primarily established through molecular data. Molecular phylogenies support its recognition as a valid species, which is distributed across Colombia, Ecuador, northeastern Peru, and Venezuela (Velazco et al. 2010).

Bats are considered particularly sensitive to climate change due to their high surface-area-to-volume ratios, which increase susceptibility to dehydration, and their generally low reproductive rates (Festa et al. 2023). Climate change may shift the geographic ranges of bat species, facilitating colonization of new areas while also leading to local extirpations from previously suitable habitats (Silva et al. 2023). In the Neotropics, the combined effects of deforestation and climate change pose substantial threats to biodiversity. Specialist species—those with narrow dietary niches and specific habitat requirements for roosting and foraging—are particularly vulnerable to these environmental changes (Clavel et al. 2011). Conversely, generalist species that exploit a wide range of resources and tolerate diverse environmental conditions may experience range expansions and increased population densities under changing conditions (Gonçalves et al. 2017; Farneda et al. 2020). Therefore, understanding how environmental changes differentially affect species based on their ecological traits is essential for identifying vulnerable taxa and prioritizing conservation efforts.

According to Velazco et al. (2010), *P. angustirostris* occurs in eastern Colombia, with confirmed records in the departments of Antioquia (northern Central Cordillera), Cundinamarca, Boyacá (eastern Andean range), and Meta (foothills of the eastern plains) (Solari et al. 2013). Despite this distribution, *P. angustirostris* remains poorly understood, largely due to its morphological similarity to co-occurring species such as *P. helleri* and *P. incarum*. Given this taxonomic ambiguity and its potential conservation concerns, the aim of this study was to model the species' current potential distribution and identify key environmental variables associated with its range. The resulting information is intended to support conservation planning for *P. angustirostris*, particularly in the context of ongoing habitat loss and fragmentation.

## METHODS

This study was conducted as part of an evaluation of the bat fauna in the Upper Magdalena River Valley, Colombia. All bat handling and specimen collection followed the ethical guidelines established by the American Society of Mammalogists (Sikes et al. 2019). Voucher specimens were preserved through the preparation of study skins and cleaned skulls, and deposited in the Mammal Section of the Zoological Collection of the Universidad del Tolima (CZUT-M 1420 and 1421).

Fieldwork was authorized by the Colombian environmental authority (Autoridad Nacional de Licencias Ambientales, ANLA) under research permit no. 02252, issued on 14 November 2019. Two adult males of *Platyrrhinus angustirostris* were captured using a 12 × 2.5 m mist net deployed at ground level in a recovering secondary vegetation area, formerly used for intensive livestock grazing. The site is located on the northern slope of the Magdalena River, approximately 85 km along the road connecting Ibagué to Armero Guayabal, Tolima Department, Colombia.

The regional climate corresponds to tropical dry forest, with a mean annual temperature of 27 °C, annual precipitation of 1,738 mm, and elevations ranging from 250 to 275 m a.s.l. (Cortolima 2011). Soils in the area are sandy-loam in texture, moderately acidic, with organic matter content ranging from 0.5% to 1.1%, and support optimal vegetation development (Torres et al. 2017). During the sampling period, other bat species recorded included *Artibeus lituratus* Olfers, 1818; *A. planirostris* (Spix, 1823); *A. phaeotis* (Miller, 1902); *Carollia castanea* Allen (1890), *C. perspicillata* Linnaeus, 1758; *Mesophylla macconnelli* Thomas, 1901 and *Uroderma convexum* Lyon (1902).

To model the potential distribution of *P. angustirostris* in Colombia, we compiled occurrence records from specimens deposited in the following biological collections: Zoological Collection of Universidad del Tolima (CZUT-M, Colombia), Institute of Natural Sciences of Universidad Nacional de Colombia (ICN), Zoological Collection of Universidad de Santa Rosa de Cabal (CUSM, Colombia), Field Museum of Natural History (FMNH, USA), and the United States National Museum (USNM, now the National Museum of Natural History, USA). From specimen labels, we extracted geographic coordinates, elevation, locality, and corresponding life zones following Holdridge's classification (1987) (Table 1).

We used an elevation raster and 19 bioclimatic variables (bio_1 to bio_19) obtained from WorldClim v. 2.1 (1970–2000) at 2.5 arc-minute resolution, downloaded using the raster::getData function in R (Fick and Hijmans 2017). These environmental variables served as predictors for modeling the species' ecological niche.

The model was generated using the MaxEnt algorithm (v. 3.4.1) with default parameters. We assessed

**Table 1.** Records of *Platyrrhinus angustirostris* in Colombia used for modeling the potential distribution of the species. The new records are in bold.

| Voucher | Latitude | Longitude | Elevation a.s.l. (m) | Municipality | Department | Life zones | Regions |
|---|---|---|---|---|---|---|---|
| ICN 14915 | –04.1925 | –069.9393 | 100 | Leticia | Amazonas | THF | AM |
| USNM 432913 | 07.9129 | –076.7371 | 3 | Chigorodó | Antioquia | THF | |
| USNM 499873, 499874, 499876, 499877, 499879, 499882, 499898, 499899, 499900 | 05.7732 | –075.8922 | 1257 | El Aljibe | Antioquia | LMHF | AN |
| USNM 499453, 499454, 499456 | 07.3029 | –075.0702 | 465 | La Tirana | Antioquia | THF | AN |
| USNM 499444 | 07.2741 | –075.2072 | 620 | Taraza, Buenos Aires | Antioquia | THF | AN |
| USNM 499885 | 07.3198 | –075.0531 | 357 | Providencia, 23 km al S, 22 km al O. Zaragoza | Antioquia | THF | AN |
| FMNH 49156 | 04.9667 | –074.4333 | 1132 | Sasaima | Cundinamarca | HPF | OR |
| USNM 507188 | 04.1466 | –073.6495 | 562 | Villavicencio | Meta | THF | OR |
| ICN 13753, 13755 | 00.0311 | –075.2857 | 217 | Puerto Leguízamo | Putumayo | THF | AM |
| **CZUT–M 1420, 1421** | **04.9993** | **–074.9073** | **282** | **Armero Guayabal** | **Tolima** | **TDF** | **AN** |
| CUSM 67 | 04.1976 | –075.8706 | 1200 | Belén de Umbría | Risaralda | HPF | AN |
| CUSM 312 | 04.7744 | –075.7837 | 1193 | Pereira | Risaralda | HPF | AN |
| CUSM 321 | 04.9520 | –075.7166 | 1180 | Marsella | Risaralda | HPF | AN |
| CUSM 327 | 05.0588 | –705.9691 | 900 | Santuario | Risaralda | HPF | AN |

ICN: Instituto de Ciencias Naturales, Universidad Nacional de Colombia; USNM: National Museum of Natural History; FMNH: The Field Museum of Natural History; CUSM: Colección de Historia Natural de la Universidad de Santa Rosa de Cabal, Colombia and CZUT: Colección Zoológica de la Universidad del Tolima, Colombia; THF: Tropical Humid Forest; LMHF: Lower Montane Humid Forest, HPF: Humid–Premontane Forest, TDF: Tropical Dry Forest, AM: Amazon, AN: Andean, and OR: Orinoquia.

species presence across different geographic regions and the Andean corridor of Colombia using 10 replicates. Final predictions were based on the mean habitat suitability maps (Hoveka et al. 2016). The dataset was randomly partitioned into 80% for training and 20% for testing.

To reduce multicollinearity and improve model performance, we calculated variance inflation factors (VIF). Variables with VIF > 4.5 were excluded (Chatterjee and Hadi 2006), resulting in a final selection of 10 predictors for model construction (Table 2). The relative contribution of each predictor was assessed using the percent contribution and jackknife test (Phillips et al. 2006), which is particularly effective for small sample sizes (Pearson et al. 2007).

Model accuracy test: we evaluated model performance using the receiver operating characteristic (ROC) curve analysis. The ROC curve plots the true positive rate (sensitivity) against the false positive rate (1-specificity), and the area under the curve (AUC) indicates model accuracy. AUC values range from 0 to 1, where higher values represent stronger predictive performance and a greater association between environmental variables and species occurrence (Zhang et al. 2021).

**Table 2.** The percentage contribution of the ten selected bioclimatic variables for the potential distribution of *Platyrrhinus angustirostris* in Colombia based on Jackknife tests.

| Variable | Code/Unit | Contribution (%) |
|---|---|---|
| Isothermality (BIO2/BIO7) (X 100) | Bio3 | 63.1 |
| Precipitation of the Warmest Quarter | Bio18 (mm) | 11 |
| Temperature Seasonality (Standard deviation X100) | Bio4 (ºC) | 8.4 |
| Precipitation Seasonality (Coefficient of Variation) | Bio15 | 7.2 |
| Precipitation of the Driest Quarter | Bio17 (mm) | 5.0 |
| Precipitation of the Coldest Quarter | Bio19 (mm) | 1.9 |
| Mean Diurnal Range (Mean of monthly (max temp – min temp) | Bio2 (ºC) | 2.6 |
| Mean Temp. of the Warmest Quarter | Bio10 (ºC) | 0.5 |
| Mean Temp. of the Driest Quarter | Bio9 (ºC) | 0.3 |
| Precipitation of the Driest Month | Bio14 (mm) | 0.1 |

## RESULTS

***Platyrrhinus angustirostris* Velazco, Gardner & Patterson, 2010**
Figures 1, 2

**New record** (Figure 3). COLOMBIA — Tolima • Armero Guayabal (Centro Universitario Regional del Norte); 04°59'59"N, 074°54'27"W; 265 m elev.; 21 Nov. 2013; L.V. García-Herrera & L.A. Ramírez-Fráncel leg.; secondary forest / tropical dry forest / mist nets; Two male specimens: CZUT-M 1420 & 1421.

**Identification.** Our specimens exhibit diagnostic characteristics of *P. angustirostris* proposed by Velazco et al. (2010). The skull and forearm measurements of the two specimens reported here are within the range of the type series (Table 3).

The specimens have the following external diagnostic characters of *P. angustirostris*: dorsal pelage bicolored, with dark tips; ventral pelage dark gray; facial lines narrow, white; dorsal strip narrow, white; inter-

**Figure 1.** Adult male of *Platyrrhinus angustirostris* (CZUT-M 1420) in dorsal and ventral views, captured in Armero Guayabal, Department of Tolima, Colombia.

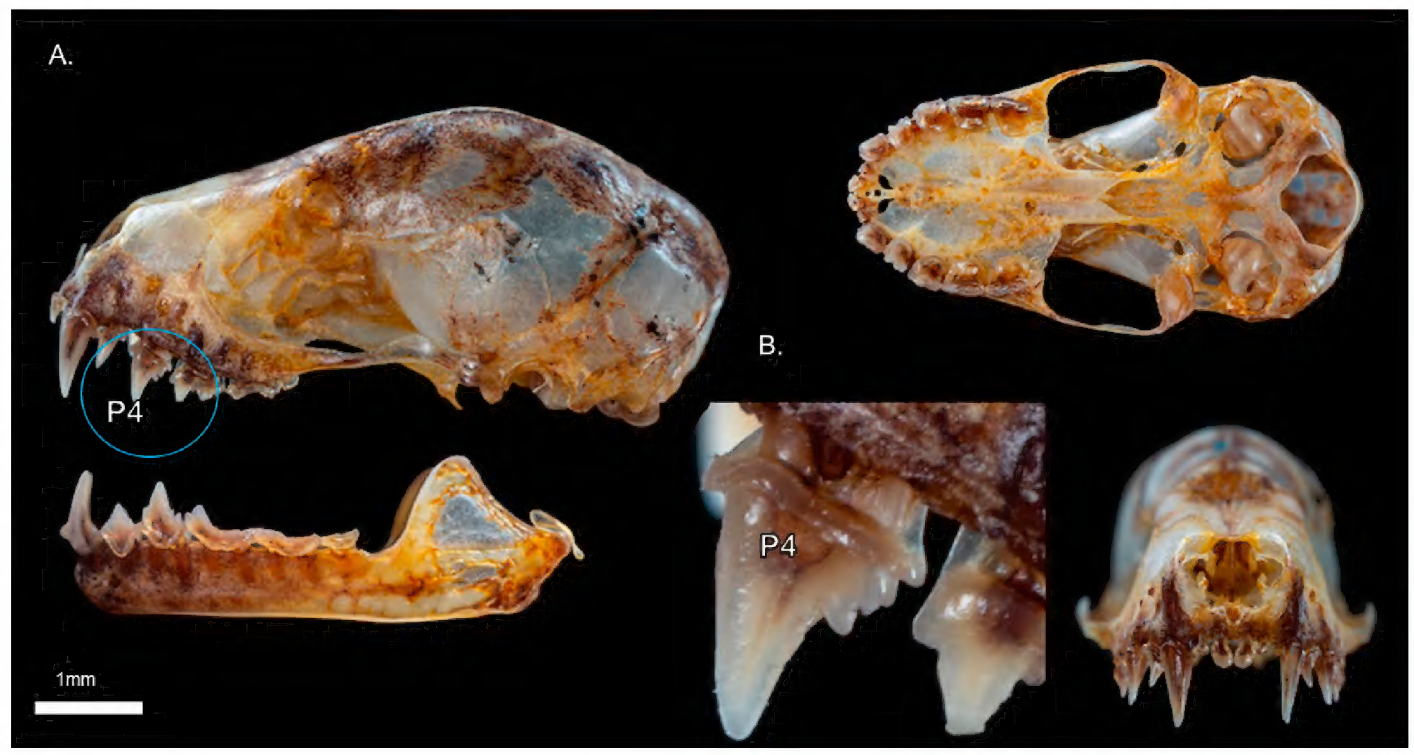


**Figure 2. A.** Anterior, ventral, and occlusal views of the skull and jaw of a male of *Platyrrhinus angustirostris* (CZUT-M 1420) captured in Armero Guayabal, Department of Tolima, Colombia. **B.** Lateral view of the skull showing three cuspules on the posterior cristid of P4.

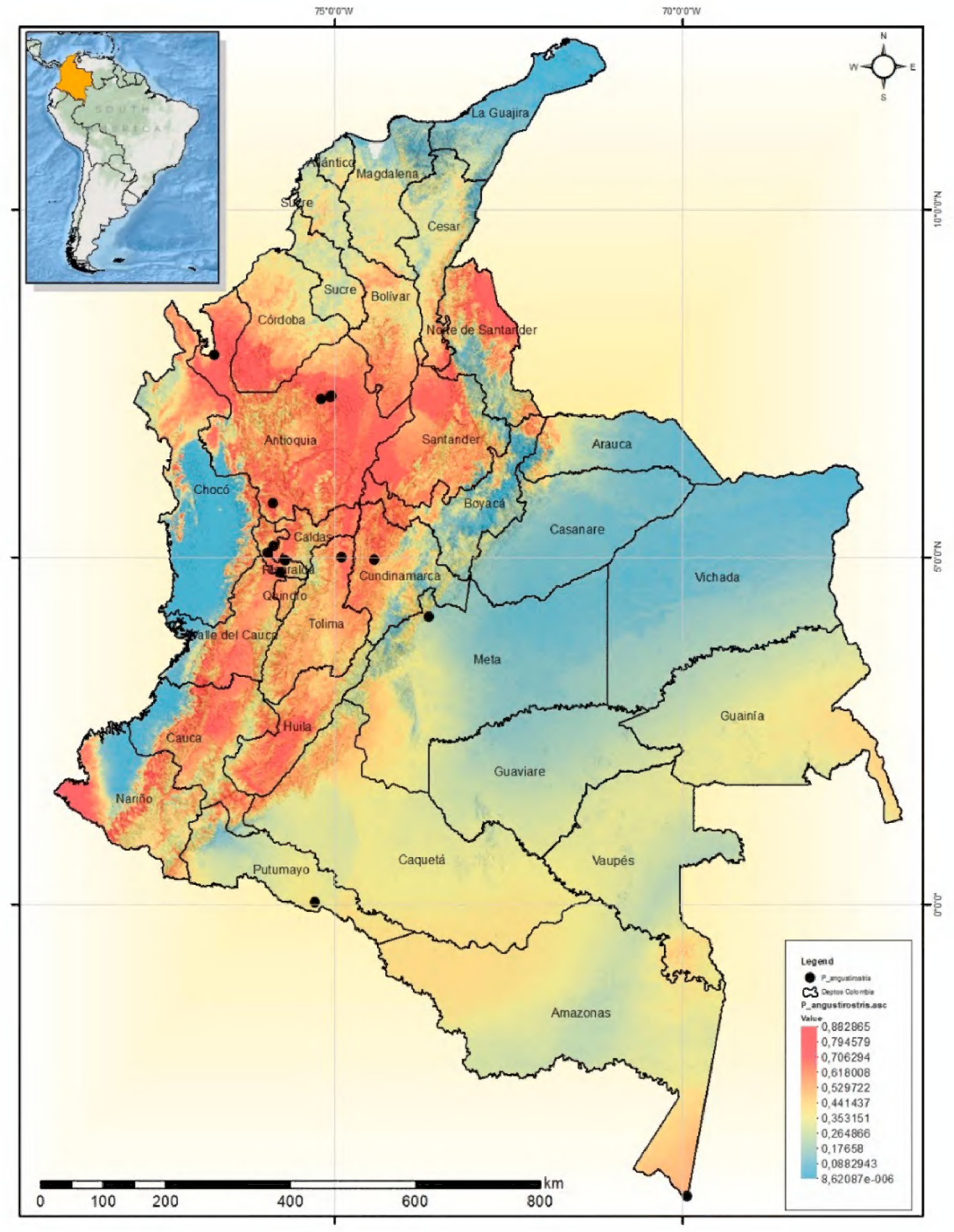


**Figure 3.** Distribution of *Platyrrhinus angustirostris* in Colombia based on the voucher records in selected collections (colors dots) and new records (bold dots). Habitat suitability classes ranging on unsuitable (cooler blue), low potential, moderate potential, and high potential (hotter red).

femoral membrane shaped like an inverted U and densely haired; metacarpal V shorter than metacarpal III; plagiopatagium inserted onto metatarsal I (Figure 1). Our specimens have a thin skull; rostrum narrow, shallow rostrum (Table 3); posterior edge of the hard palate shaped as an inverted V; postorbital processes moderately developed; internal upper incisors converging but not in contact, with tips extending under the upper canine cingula; P4 with three cusps on the proximal side (Figure 2).

The habitat at the site of capture is dominated by scrubland covered by *Calliandra pittieri, Cecropia peltata*, *Centrosema pubescens, Cordia alliodora, Crataeva tapia, Croton schiedeanus, Solanum betaceum*, and *Solanum nigrum*. This site, currently being recovered following intense mining and livestock raising.

The map produced using MaxEnt MaxEnt is shown in Figure 3; it reflects the degrees of habitat suitability for the species, and its current potential distribution is associated with the Colombian Andean region, which comprises 24.5% of the country's land surface (Etter and van Wyngaarden 2000) and includes the western, central, and eastern mountain ranges and a large part of the Magdalena and Cauca River valleys. This region is characterized by a mosaic of ecological regions of savannah tropical forests and wooded areas with diverse topography, climate, and vegetation (Fernández-Méndez et al. 2016). In addition, large agricultural extensions and socio-ecological dynamics have historically generated deforestation in several regions of the Colombian Andes (Sierra et al. 2017).

We evaluated the accuracy of the MaxEnt model. Our models showed high levels of predictive performance, with AUC (training 0.984 ± 0.001; test 0.956 ± 0.009) and AUCDiff (0.010 ± 0.006) indicating a good performance with low levels of errors and correctly identifying all the localities where the species has been reported (Figure 4). In this study, the AUC values of training data and verification data are 0.85, indicating that

**Table 3.** Measurements (mm) of *Platyrrhinus angustirostris* specimens reported here (CZUT-M) and of the type series (Velazco 2010).

| Trait | Holotype FMNH 129150 ♂ | Paratype FMNH 129152 ♂ | This study CZUT–M | |
|---|---|---|---|---|
| | | | 1420 ♂ | 1421 ♂ |
| GLS | 20.9 | 20.8 | 21.7 | 21.96 |
| CIL | 18.9 | 18.6 | 18.09 | 17.64 |
| BB | 8.8 | 9.2 | 9.68 | 9.51 |
| ZB | 11.6 | 11.7 | 11.37 | 11.22 |
| PB | 5.0 | 5.4 | 5.7 | 5.6 |
| MB | 9.3 | 9.7 | 10.31 | 10.24 |
| MTRL | 7.3 | 7.0 | 7.95 | 7.83 |
| M2–M2 | 1.8 | 1.8 | 1.8 | 1.7 |
| DENL | 13.6 | 13.6 | 14.5 | 14.1 |
| MANDL | 8.0 | 7.7 | 8.84 | 8.96 |
| FA | 39.0 | 35.1 | 41.8 | 36.83 |

GLS: greatest length of skull; CIL: condyloincisive length; BB: braincase breadth; ZB: zygomatic breadth; PB: postorbital breadth; MB: mastoid breadth; MTRL: maxillary toothrow length; M2–M2: width across second upper molars; DENL: length of dentary. distance from midpoint of mandibular condyle to anterior–most margin of dentary; MANDL: length of mandibular toothrow; FA: forearm length. FMNH: Field Museum of Natural History. CZUT-M: Colección Zoológica de la Universidad del Tolima, Ibagué, Colombia.

the MaxEnt model is very effective in predicting the potential distribution of *P. angustirostris*. The predicted geographical distribution results and the actual distribution have a high degree of overlap between the regions, which means the results can be applied to the suitable regionalization of this species.

For a weighted analysis of dominant environmental variables, the Jackknife method was used in the MaxEnt model, and the results show the weight of different environmental factors affecting the habitat suitability of *P. angustirostris* (Figure 5). The vertical axis represents the screened environmental variables, and the horizontal axis represents the score of each environmental variable. The dark blue column represents the model score with only this environmental factor, the light-blue column represents the sum of the scores of other variables except for this variable, and red represents the sum of all variables' scores. The main environmental factors affecting the potential distribution of *P. angustirostris* were isothermality, precipitation of the warmest quarter, temperature seasonality, precipitation seasonality, and precipitation of the driest quarter (Table 2). The contribution rates are 63.05; 11.0; 8.40; 7.2 and 5%, respectively, and the total contribution rate was 94.65%.

The modeling procedure made it possible to identify a number of factors that potentially affect the spatial distribution of *P. angustirostris*. In the course of the model training, three variables turned out to make the greatest contribution (in percentage points) to the modeling: isothermality (temperature variation) for the

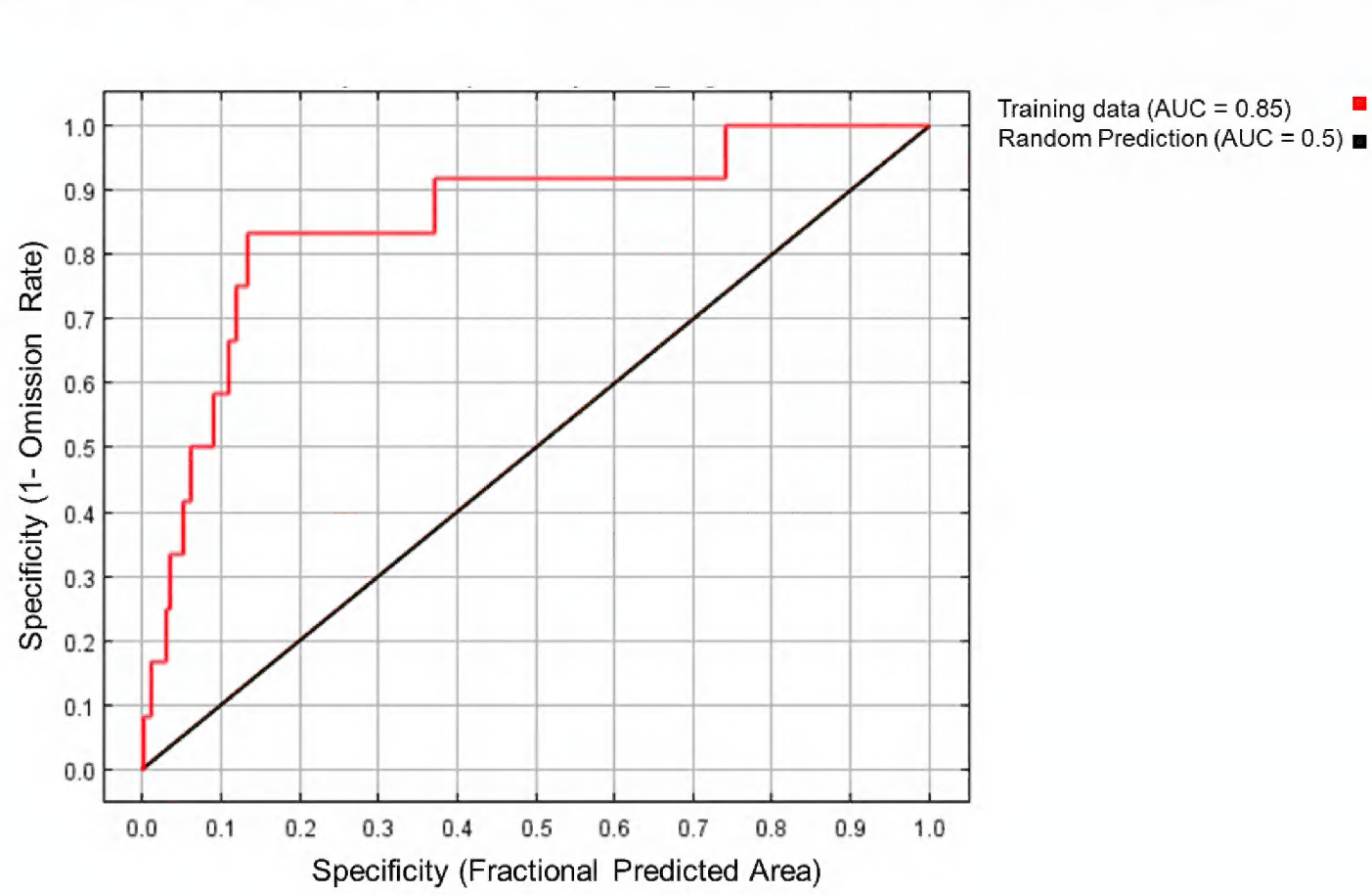


**Figure 4**. Receiver operating characteristic (ROC) curve and AUC values of the MaxEnt model. The red curve indicates training data and the black line indicates random prediction.

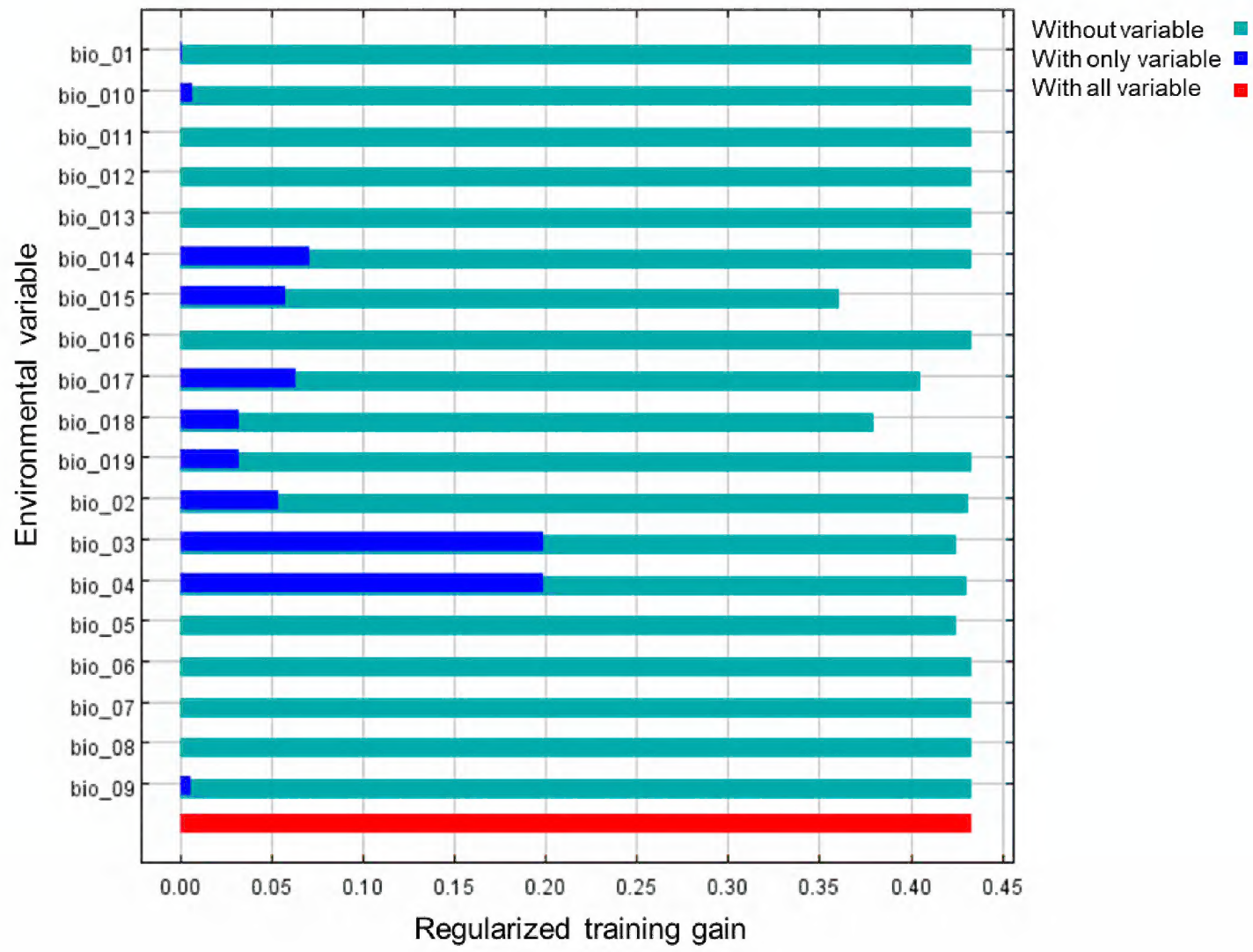


**Figure 5.** Global potential distribution prediction of *Platyrrhinus angustirostris* based on resulting MaxEnt model.

presence of the species is 95 units, with a probability of distribution of 0.71, which is reduced to 0.15 in areas with values below 65 units (Figure 6A). The precipitation of the warmest quarter it must range between 1800 and 2000 for the probability of occurrence of the species to be greater than 95% (Figure 6B) and with temperature seasonality less than or equal to 20%, a probability of presence between 0.65 and 0.95 was estimated (Figure 6C).

The model predicts a continuous distribution range in the Colombian Andean region, across the three cordilleras (western, central and eastern), from the south in Nudo de los Pastos north to the Catatumbo subregion in the Department of Norte de Santander (see Figure 3).

## DISCUSSION

Prior to the revision by Velazco et al. (2010), *Platyrrhinus angustirostris* was undifferentiated under *P. helleri*, and therefore, specific information on its conservation status was unavailable. Although the 2016 Interna-

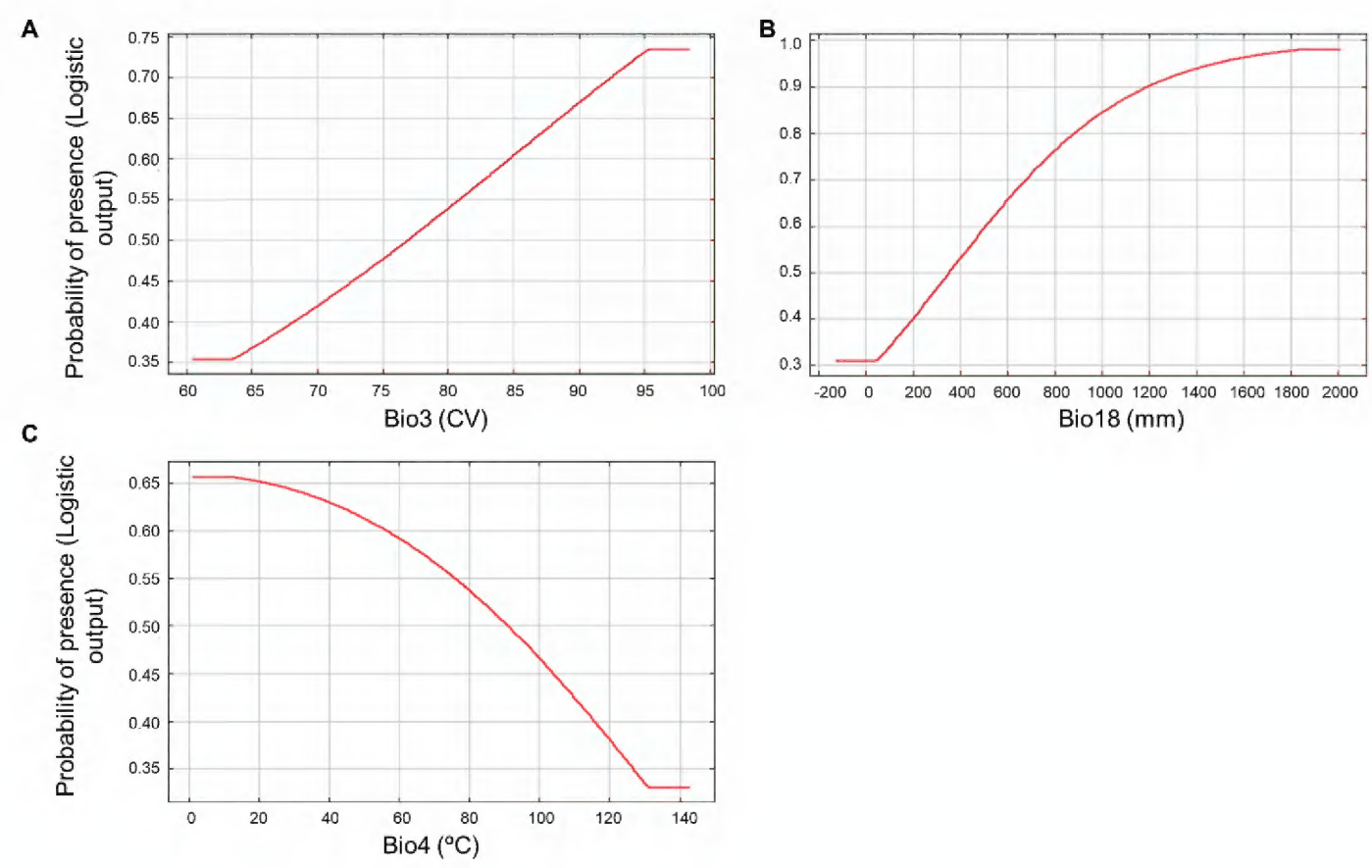


**Figure 6.** Bioclimatic variables with the greatest contribution to maximum entropy modeling for *Platyrrhinus angustirostris* in Colombia. **A.** Isothermality (temperature variation). **B.** Precipitation of the warmest quarter. **C.** Temperature Seasonality.

tional Union for the Conservation of Nature (IUCN) Red List categorized *P. angustirostris* as Least Concern (Solari 2017), this assessment should be considered a starting point rather than a definitive assessment. The species' current conservation status should be regarded as uncertain, particularly given that its populations inhabit areas increasingly affected by deforestation and the expansion of agricultural and livestock-ranching frontiers. Consequently, a more precise and updated reassessment is urgently needed.

Our results update and predict a broader distribution range for *P. angustirostris* in Colombia. To the best of our knowledge, this is the first documented record of the species on the eastern slope of the Central Andes in Colombia. Existing records of the species correspond to three life zones tropical humid forest, lower montane humid forest, and humid premontane forest, and we report a new life zone: the tropical dry forest. Unfortunately, tropical dry forests have the third-highest deforestation rate globally and are subject to intense anthropogenic disturbance (Coelho et al. 2017; Stan and Sánchez-Azofeifa 2019). Much of this deforestation is due to anthropogenic use of land for raising cattle, agriculture, and selective logging, which are socioeconomic activities that have caused landscape modifications to the dry forests throughout Latin American countries. Such modifications create new landscapes with scattered forest fragments of different sizes and at different successional stages (Stan and Sánchez-Azofeifa 2019).

In Colombia, tropical dry forests are undergoing continuous degradation due to a combination of hunting, selective logging, land clearing by fire for agriculture and cattle ranching, and mining activities. These pressures have led to the loss of over 60% of the original forest cover (Pizano and García 2014; González-M. et al. 2018). Consequently, this biome has been classified as Critically Endangered according to IUCN criteria (Buzzard et al. 2016).

Under current climatic conditions, our model indicates that the areas with the highest environmental suitability for *P. angustirostris* are concentrated in the north-central region of Colombia, suggesting that this distribution reflects optimal climatic conditions for the species. Nonetheless, conservation efforts are imperative to protect the life zones where the species occurs, especially given the ongoing loss of forest cover and reduced landscape connectivity. Our results highlight the Norandina biogeographic province—including the departments of Antioquia, Caldas, Cundinamarca, Huila, Risaralda, Tolima, Quindío, and Valle del Cauca—as the area with the highest predicted probability of occurrence. The model also predicts significant suitability in the Chocó–Magdalena region. These patterns suggest that the distribution of *P. angustirostris* is closely tied to ecological associations between the Magdalena and Cauca river valleys—regions that serve as transition zones facilitating biotic interchange between cis-Andean and inter-Andean areas. Similar distributional patterns have been documented in various animal groups, including bats (Hernández-Camacho et al. 1992; Mantilla-Meluk et al. 2009).

Among the environmental variables analyzed, isothermality (BIO3) and precipitation during the warmest quarter (BIO18) exhibited the greatest explanatory power in modeling the potential distribution of *P. angustirostris*. Isothermality measures the ratio of diurnal to annual temperature variation, with higher values indicating regions where day-to-night temperature changes closely resemble seasonal temperature fluctuations (Noguera-Urbano and Ferro 2018). In such isothermal regions, thermal conditions remain relatively stable year-round.

These findings align with broader ecological principles governing Neotropical mammal endemism, where topographic heterogeneity and moderate thermal variability are primary determinants of species distributions (Noguera-Urbano and Ferro 2018). The data presented here contribute novel insights into the habitat preferences and geographic distribution of *P. angustirostris* within the Colombian Andes. This information serves as a critical foundation for developing targeted conservation strategies for this poorly known species and the tropical ecosystems it inhabits.

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## ADDITIONAL INFORMATION

### Conflict of interest

The authors declare no conflict of interest.

## Ethical statement

Statement on the welfare of animals included all applicable international, national and/or institutional guidelines for the care and use of animals were followed.

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## Author contributions

Conceptualization: LVG, LAR. Data curation: LVG. Formal analysis: LVG, LAR. Investigation: LVG, LAR. Methodology: LVG, LAR, GG. Supervision: LMF, GG, BLK. Validation: BLK. Writing – original draft: LVG, LAR, GG, LMF. Writing – review and editing: LVG, LAR, GG, LMF. BLK.

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## Data availability

All data that support the findings of this study are available in the main text and Supplementary materials.

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